



Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at <http://about.jstor.org/participate-jstor/individuals/early-journal-content>.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

AMERICAN JOURNAL OF BOTANY

VOL. II

JANUARY, 1915

No. 1

INVESTIGATIONS ON THE PHYLOGENY OF THE ANGIOSPERMS

5. FOLIAR EVIDENCE AS TO THE ANCESTRY AND EARLY CLIMATIC ENVIRONMENT OF THE ANGIOSPERMS

EDMUND W. SINNOTT AND IRVING W. BAILEY

The leaf of the Angiosperms is so variable in its shape and venation among closely related species and so easily modified by environmental influences that gross foliar characters have been largely neglected by the taxonomist and the phylogenist except within small groups of plants. A careful survey of evidence obtained from the various botanical fields, however, apparently makes possible a reconstruction of the primitive Angiosperm leaf with a reasonable degree of certainty, and a determination of some of the factors which have modified it; and thus suggests not alone the probable ancestry of the Angiosperms but also the climatic conditions under which they first appeared. The presentation of evidence on which such an hypothesis may be built is the purpose of the present paper.

It is with the more ancient of the two Angiosperm classes, the Dicotyledons, that the problem necessarily rests. The two main types of leaf venation in this group are the palmate and the pinnate, between which intermediate conditions frequently occur. Leaf shape is, of course, generally correlated with venation although there are numerous instances where broad leaves are pinnate and narrow ones palmate. The main leaf types, having reference both to venation and shape, may be roughly designated as the palmate simple (fig. 2),

[The *Journal* for December (1 : 499-550) was issued 29 Dec. 1914.]

palmate lobed (fig. 3), palmate compound¹ (fig. 7), pinnate simple (fig. 1), pinnate lobed (fig. 17) and pinnate compound (fig. 10). A brief survey of the distribution of these types throughout the three main growth forms of Dicotyledons (trees, shrubs and herbs) in various regions of the earth is set forth in the following table.²

It will be observed that in these modern floras the pinnate type is markedly predominant everywhere and that the simple pinnate condition alone constitutes from 60 per cent to 70 per cent of the species. Other noteworthy facts are the abundance of compound leaves in warm regions, the almost complete absence there of palmately lobed woody plants, and the practical confinement of the pinnately lobed type to herbaceous forms.

In view of the preponderating evidence that woody Angiosperms are more ancient than herbaceous ones,³ it seems probable that leaf

¹ Trifoliate leaves with stalked terminal leaflets (frequently called pinnately trifoliate) will be regarded in this paper as palmately compound.

² Analyses have been made of the following floras as to types of leaf or types of node or both:

North America: Flora of the Northern United States and Canada, Britton and Brown; Flora of the Rocky Mountains, Coulter; Flora of the Florida Keys, Small; Flora of the British West Indian Islands, Grisebach; Flora Nicaraguensis, Goyena.

South America: Flora Brasiliensis, Martius and others; Historia de Chili: Botánica, Gay; Report of the Princeton Expedition to Patagonia: Botany, Macloskie.

Europe: English Botany, Sowerby; Flora des Nordostdeutschen Flachlands, Ascherson and Graebner; Flora Rossica, Ledebour; Flora des Alpes, Bouvier; Flora Española, Lazara; Flora Italica, Fiori and Paoletti.

Asia: Flora Orientalis, Boissier; Flora of Syria, Palestine and Sinai, Post; Flora Simlensis, Collett; Flora of the Upper Gangetic Plain, Duthie; Flora of Bombay, Cooke; Handbook of the Flora of Ceylon, Trimen; Maylayan Flora, King; Flora van Nederlandesch Indië, Miquel; Flora Hongkongensis, Bentham; Flora of Manila, Merrill.

Africa: Manual of the Flora of Egypt, Muschler; Flora of Tropical Africa, Oliver, Thiselton-Dyer and others; Flora Capensis, Harvey and Sonder, and others; Forests and Forest Flora of Cape Colony, Sims; Natal Plants, Wood; Plantes de Madagascar, Baillon and Castillo; Flora of Mauritius and the Seychelles, Baker.

Australasia: Flora Australiensis, Bentham; New Zealand Flora, Cheeseman.

Oceania: Flora of the Hawaiian Islands, Hillebrand; Indigenous Trees of the Hawaiian Islands, Rock.

Analyses were also made of the genera of woody Dicotyledons enumerated in Engler and Prantl's Natürliche Pflanzenfamilien; and of the species of trees and shrubs from China and Japan in the herbarium of the Arnold Arboretum.

³ The Origin and Dispersal of Herbaceous Angiosperms. Sinnott, E. W. and Bailey, I. W., Annals of Botany, 28: Oct. 1914.

TABLE I

		Palm. S.	Palm. L.	Palm. C.	Pinn. S.	Pinn. L.	Pinn. C.
		%	%	%	%	%	%
<i>Engler</i>							
<i>Tropical Regions</i>							
Trees.....	1,326 genera	6	2	4	62	—	26
Shrubs.....	1,257 "	14	1	3	69	—	12
<i>Temperate Regions</i>							
Trees.....	273 "	8	6	5	60	1	19
Shrubs.....	776 "	7	2	5	76	2	8
<i>N. United States..... 2,821 sps. ..</i>							
Trees.....	163.....	7	6	3	57	8	19
Shrubs.....	328.....	5	9	8	72	—	7
Herbs.....	2,330.....	11	4	10	58	6	10
<i>Great Britain..... 1,310 sps.</i>							
Trees.....	73.....	7	5	—	78	4	6
Shrubs.....	136.....	1	7	15	63	—	14
Herbs.....	1,101.....	8	7	8	56	9	12
<i>Italy..... 3,079 sps.</i>							
Trees.....	72.....	13	11	5	48	6	13
Shrubs.....	306.....	4	9	12	55	1	19
Herbs.....	2,701.....	5	5	13	56	11	10
<i>China..... 2,075 sps.</i>							
Trees.....	501.....	14	10	3	56	—	17
Shrubs.....	1,574.....	10	6	11	62	—	11
<i>Japan..... 542 sps.</i>							
Trees.....	174.....	12	14	2	60	—	11
Shrubs.....	347.....	7	7	13	66	—	7
<i>Amazon Valley..... 2 187 sps.</i>							
Trees.....	941.....	3	.5	6	66	—	24
Shrubs.....	1,068.....	19	.5	6	65	—	9
Herbs.....	178.....	25	5	8	56	3	3
<i>Madagascar..... 539 sps.</i>							
Woody Plants.....		11	1	4	73	—	11
<i>Hawaii..... 211 sps.</i>							
Trees.....		8	1	4	76	—	11
<i>Cape Colony..... 380 sps.</i>							
Trees.....		9	—	10	68	1	12
<i>Natal..... 303 sps.</i>							
Trees.....	50.....	10	—	6	64	—	20
Shrubs.....	139.....	3	4	11	72	—	10
Herbs.....	114.....	6	13	6	66	8	1

modifications among herbs are often of very recent origin and that the important steps in the foliar evolution of the Dicotyledons took place while they were practically all woody in habit.

Evidence from various sources as to the relative antiquity of the six leaf types may be outlined as follows.

PALAEOBOTANICAL EVIDENCE

Analyses of leaf type in various Cretaceous and Tertiary dicotyledonous floras have been made and are presented in the following table.⁴ Owing to the frequent impossibility of determining whether an impression is that of a palmately or pinnately compound leaf, all the compound species have been thrown together. For simplicity's sake the few pinnate lobed forms have been included with the pinnate simple ones.

It will be noted that the percentage of compound leaves in the fossil floras is smaller than in the modern ones. This is probably due in part to the fact that compound leaves are usually broken up in fossilization into their component leaflets, which have often been described as complete leaves. The most striking difference, however, between ancient and present day floras is the much greater abundance in the former of palmate leaves (32 per cent as against 13 per cent in living species). In the Cretaceous the palmate-lobed forms were as numerous as the simple ones. In the Tertiary the lobed type was

⁴ The following fossil floras have been examined:

Cretaceous: The Lower Cretaceous Deposits of Maryland, Berry (and others). Maryland Geological Survey; The Upper Cretaceous and Eocene Floras of South Carolina and Georgia, Berry. Professional Paper 84, U. S. G. S.; Flora of the Dakota Group, Lesquereux, Geol. Surv. of the Territories, Vol. VIII; Cretaceous Flora of the Territories, Lesquereux, Geol. Surv. of the Territories, Vol. VI; Flora of the Raritan Formation, Berry, Bull. 3, Geol. Surv. of New Jersey; Flora of the Amboy Clays, Newberry, Monograph XXVI, U. S. G. S.; Cretaceous Floras of Southern New York and New England, Hollick, Monograph L., U. S. G. S.; Flora Fossilis Arctica, Heer, including the Arctic, Patoot and Atane floras (Cretaceous) and those of the Polar Lands, Greenland, North Greenland, and Spitzbergen (Tertiary).

Tertiary. The Tertiary Flora of the Western Territories, Lesquereux, Geol. Surv. of the Territories, Vol. VII; The Flora of the Laramie Group, Ward, 6th Ann. Report, U. S. G. S.; The Flora of the Bad Lands, Lesquereux, Geol. Surv. of the Territories, Vol. VIII; Flore Fossile des Travertins Anciens de Sezanne, Saporta, Mem. Soc. Geol. de France (2), VIII; Tertiarfloren der Oesterr. Monarchie, Ettinghausen, Vienna, 1851; La Flore Fossile du Japon, Nathorst, Bih. Svensk. Vetensk. Akad. Handlingar, B. 20, No. 2.

TABLE II

	Species	Palm. Simple	Palm. Lobed	Pinnate	Compound
<i>Cretaceous</i>					
Potomac.....	22	6	7	6	3
S. Carol. and Georgia.	68	11	3	46	8
Dakota.....	163	24	42	95	2
Territories.....	79	19	20	39	1
Raritan.....	114	12	14	75	13
Amboy Clays.....	106	15	16	67	8
S. N. Y. and N. Eng..	159	22	22	107	8
Arctic.....	32	3	1	20	8
Patoot.....	71	14	8	37	12
Atane.....	94	15	8	47	24
Total.....	908	141 (15.5%)	141 (15.5%)	539 (59%)	87 (10%)
<i>Tertiary</i>					
Territories.....	205	57	12	109	27
Laramie.....	130	46	8	68	8
Bad Lands.....	34	12	6	10	6
Polar Lands.....	84	24	3	48	9
Greenland.....	178	31	11	106	30
N. Greenland.....	46	13	4	24	5
Spitzbergen.....	50	17	5	26	2
Sezanne.....	70	19	3	40	8
Austria.....	31	3	4	18	6
Japan.....	49	7	5	30	7
Total.....	877	229 (26%)	61 (7%)	479 (55%)	106 (12%)
Total of fossil floras studied.....	1,785	370 (21%)	202 (11%)	1,018 (57%)	195 (11%)
Total woody plants in modern floras studied	7,014	661 (9%)	305 (4%)	4,578 (65%)	1,470 (21%)

little commoner than at present, but the palmate simple was much more abundant. Of course other fossil floras which are yet to be worked out, particularly those which are distinctly from tropical regions (where palmate forms are generally less numerous) may sometimes show conditions different from those which we have presented here; and fossil evidence in the present problem cannot be regarded as at all conclusive. The facts available at present, however, certainly seem to indicate that palmate leaves, particularly lobed ones, were much more abundant in earlier geologic time than at present.

MORPHOLOGICAL EVIDENCE

1. *The Node*.—Important evidence toward a solution of the present problem may be obtained from a study of the general topography of the node. One of the writers⁵ has shown that among Dicotyledons

⁵ The Anatomy of the Node as an Aid in the Classification of Angiosperms. Sinnott, E. W., Am. Jour. Botany, 1: 303-322. 1914.

the vascular supply to the leaf causes either a single gap (unilacunar type, fig. 85), three gaps (trilacunar type, figs. 83 and 84), or more than three gaps; that these types are very constant within large groups of plants, and that the trilacunar condition is probably the most ancient of all, the other two having been derived from it by amplification or reduction. It is pointed out that the main distinction lies really between the tri- and multilacunar, on the one hand (which in this paper we shall designate together as multilacunar), and the unilacunar on the other. That the former type is almost certainly more ancient than the latter is made evident by the fact that it characterizes the vast majority of all those orders (Amentiferae, Ranales, Rosales and Malvales) which are recognized as being relatively ancient and among which are presumably to be found the most primitive living Dicotyledons. The following table, based on the genera of Dicotyledons enumerated by Engler, also shows the distribution of these two nodal types among the trees, shrubs and herbs of the Archichlamydeae and Metachlamydeae.⁶

TABLE III

Genera.	Multilacunar.	Unilacunar.
<i>Archichlamydeae</i>		
Trees.....	972, 76%.....	909, 24%
Shrubs.....	794, 71%.....	322, 29%
Herbs.....	688, 59%.....	466, 41%
<i>Metachlamydeae</i>		
Trees.....	19, 6%.....	269, 94%
Shrubs.....	199, 20%.....	767, 80%
Herbs.....	752, 43%.....	994, 57%
<i>Metachlamydeae, excl. Compositae</i>		
Trees.....	4, 1%.....	269, 99%
Shrubs.....	26, 3%.....	767, 97%
Herbs.....	134, 10%.....	994, 90%

It is evident that the great majority of the Metachlamydeae (especially if we exclude the Compositae) are unilacunar and that the multilacunar forms are massed in the Archichlamydeae. The contrast is much more striking among woody plants (which are really the only ones significant in our problem) than among herbs. This predominance of the multilacunar node among the older orders and in the more primitive of the two great subclasses; and the con-

⁶ Analyses of nodal type are based on a study of a very large number of species in about 700 genera, from practically all the families.

finement of the unilacunar type for the most part to less primitive groups, provide convincing evidence that the former condition is more ancient than the latter.

The importance of this conclusion is evident when we observe that there is a definite correlation between nodal topography and leaf type. This is indicated briefly for certain representative floras in the following table.

TABLE IV

	Palm. S.		Palm. L.		Palm. C.		Pinn. S.		Pinn. L.		Pinn. C.	
	Multi.	Uni.	Multi.	Uni.	Multi.	Uni.	Multi.	Uni.	Multi.	Uni.	Multi.	Uni.
	%	%	%	%	%	%	%	%	%	%	%	%
Tropical tree genera (Engler).....	64	36	100	0	94	6	47	53	100	0	93	7
Temperate tree genera (Engler).....	87	13	100	0	93	7	52	48	100	0	97	3
Northern United States												
Woody plants.....	92	8	100	0	97	3	65	35	100	0	86	14
Herbs.....	69	33	94	6	95	5	42	58	67	33	90	10
Great Britain												
Woody plants.....	100	0	100	0	100	0	77	23	100	0	91	9
Herbs.....	54	46	88	12	99	1	36	64	79	22	95	5
Italy.												
Woody plants.....	78	22	100	0	95	5	53	47	67	33	96	4
Herbs.....	54	46	94	6	97	3	38	62	78	22	92	8
China.												
Woody plants.....	79	21	97	3	93	7	56	44	—	—	91	9
Japan.												
Woody plants.....	84	16	96	4	97	3	59	41	—	—	94	6
Amazon Valley												
Woody plants.....	26 ⁷	74 ⁷	100	0	100	0	31	69	—	—	88	12
Herbs.....	66 ⁷	34 ⁷	83	17	93	7	30	70	67	33	100	0
Hawaii.												
Trees.....	94	6	100	0	100	0	35	65	—	—	100	0
South Africa.												
Trees (Sims).....	90	10	100	0	84	16	34	66	—	—	100	0

It is apparent that among woody plants the great majority of palmate simple leaves are associated with a multilacunar node,⁸ although this is not so evident among herbs. Practically all of the palmate lobed and palmate compound leaves, in both woody and herbaceous plants, belong to multilacunar species, and only a slightly smaller percentage of the pinnately compound leaves, as well. Fully

⁷ Exclusive of Melastomaceae, Woody plants, 75—25; herbs, 80—20.

⁸ Where the node is unilacunar with this foliar type, as among the Melastomaceae and certain of the Lauraceae, Verbenaceae and others, the leaf trace, although causing but a single gap, is almost always itself divided into three strands.

half of the pinnate simple leaves, on the contrary, are connected with a unilacunar nodal type. In fact, the great majority of unilacunar plants have simple pinnate leaves. Of the 5,080 unilacunar species in the floras studied, 4,430, or 87 per cent, are characterized by foliage of this type. The pinnate-lobed type is too infrequent among woody plants to make figures derived from it of any significance. This correlation between venation and nodal topography is not surprising, since the single bundle of the unilacunar node would naturally tend to continue as a strong midrib (fig. 85), and the isolated traces of the multilacunar type would readily remain isolated and produce a palmate or compound lamina (fig. 84). In fact, the three lobes of a lobed leaf and the three leaflets of a trifoliately compound one are definitely related in their ontogeny to the point of origin of the three traces.

The definite association of the unilacunar type (which seems clearly not to be primitive) with the simple pinnate leaf certainly indicates that this leaf type, now so dominant among Angiosperms, is not at all the most ancient one. The many cases where a multilacunar node, also, is present with this foliar form are to be regarded on such a view as the persistence of an ancient character at the node when it has been lost elsewhere in the leaf.

2. *Floral Parts*.—The structure of certain supposedly conservative regions other than the node also furnishes evidence for the solution of our problem. One of these regions is the floral axis and its appendages. It is very noticeable that sepals, petals and floral bracts are often palmate in their venation when foliage leaves are otherwise. The homologies of the first two organs are still matters for debate, but bracts, at least, are almost certainly to be regarded as the morphological equivalents of leaves. A few cases of palmation in floral structures are shown in figures 25 to 36. Of course there are many instances of pinnate sepals, petals and bracts but these are very rare in families where the leaves are typically palmate; and palmate floral parts are very frequent in plants with pinnate leaves. The widespread occurrence of palmation in floral parts may be looked upon as the persistence of an ancient character which has often been lost elsewhere.

3. *The Seedling*.—The truth of the doctrine of recapitulation in its application to plants is frequently questioned at the present time but enough cases of conservatism in the seedling have been recorded to make evidence from this source worth seeking in any

such problem as the present one. A general survey of seed-leaf characters throughout the Dicotyledons, such as may conveniently be found in Lubbock's treatise on seedlings,⁹ reveals the striking fact that the cotyledonary venation in the majority of cases is palmate, very often with three main veins. Not only are palmate cotyledons present in practically all palmate-leaved species but they occur (and often predominate) in every important pinnate-leaved family, as well. Some typical cases from all of the great Dicotyledonous orders are illustrated in figures 37 to 69.

The fact that the cotyledon is often broader in proportion to its length than is the vegetative leaf cannot explain its predominant palmate venation for it will be noted that in *Acer*, *Antigonon*, *Rhus* and many others the seed leaf is much narrower, proportionally, than the vegetative one but is nevertheless provided with three or more palmate veins. Nor can the palmate condition be explained as a physiological necessity for all seedlings, for there are numerous instances where the cotyledon is pinnate in venation. Taken in connection with the primitiveness of the trilacunar node, this prevalence of three-veined palmate cotyledons among Dicotyledons of all families must be regarded as important evidence that the palmate, three-veined leaf is indeed the most ancient type for the group. Should such a conclusion be clearly established, this preponderance of palmate venation in the embryo will evidently furnish an important instance of the persistence of an ancient character in plant ontogeny and will strongly support the theory of recapitulation in its application to the Angiosperms.

A somewhat similar phenomenon is provided by the peltate leaves of *Tropaeolum* (fig. 71), *Hydrocotyle* and other plants, where the early developmental stages are strongly palmate lobed (fig. 70). That this embryonic condition is ancestral for these species is indicated by its prevalence among closely related forms.

4. *Reversions*.—There are numerous cases among plants where very vigorous growth brings about a reversion to a primitive character or intensifies its ordinary development, and it might therefore be expected that large and vigorous leaves would tend to revert to a more ancient type. In most cases there is little difference in venation among the leaves of a single plant, but numerous exceptions do occur where the largest and rankest leaves are palmate lobed whereas the

⁹ A Contribution to our Knowledge of Seedlings, Lubbock, J.

smaller ones are simple palmate or pinnate. This fact is illustrated for *Acer*, *Viburnum* and *Ampelopsis* in figures 3, 5 and 6, 18 and 19, and 20 and 21. It has been observed by the writers in practically all families possessing palmately lobed leaves. There are also cases where a vigorous twig or stool shoot will produce this type of foliage although the typical leaf for the species is simple (figs. 72 and 73).

Evidence from morphology is therefore decidedly against the claims to primitiveness of the pinnate simple and pinnate lobed types, and as between the other four is clearly in favor of the greater antiquity of one of the palmate forms. Let us see whether such phylogenetic evidence as is available will permit a further narrowing down of the field.

PHYLOGENETIC EVIDENCE

Phylogenetic evidence first supports that from other sources in pointing to the simple pinnate leaf as more recent than the others, for it is overwhelmingly predominant in the Metachlamydeae. Of the 1,245 woody genera of this subclass enumerated by Engler 1,110 are simple pinnate, or 89 per cent; and of the 4,840 metachlamydeous species in the floras analyzed above, 3,780, or 78 per cent, are simple pinnate, and 400, or 8 per cent, are pinnate lobed, a total of 86 per cent. Of the 2,150 *woody* Metachlamydeae in these floras 1,915, or 89 per cent, have simple pinnate leaves. A type of leaf so closely associated with specialized floral structures is not likely to be very primitive. On the other hand, 70 per cent of the palmate simple type, 90 per cent of the palmate lobed, 93 per cent of the palmate compound and 88 per cent of the pinnate compound are included in the Archichlamydeae.

Of the four remaining types the pinnately compound, although developed for the most part among the Archichlamydeae, is found principally in the Juglandaceae, Rosaceae, Leguminosae, Zygophyllaceae, Sapindaceae, Rutaceae, Simarubaceae, Burseraceae, Meliaceae, Anacardiaceae, Araliaceae, Umbelliferae, Bignoniaceae and Oleaceae, none of which are generally regarded as being particularly ancient families. On phylogenetic evidence, therefore, the pinnately compound leaf cannot well be considered a primitive one.

To settle our problem we should be better acquainted than at present with the phylogeny of the Angiosperms. As to just what modern families should be regarded as closest to the ancient stock

is as yet not definitely settled. All evidence now available, however, as to the structure of both vegetative and reproductive organs in the various families of the inclusive order Amentiferae seems to indicate clearly that this great group of simple-flowered plants is not ancient in type, as has frequently been supposed, but is rather to be looked upon as reduced and specialized. The prevalence of the simple pinnate leaf among its members is therefore no indication of the primitiveness of this foliar type. Those Dicotyledons which both from their wood structure and reproductive morphology are today winning recognition from phylogenists as being among the most ancient members of the whole class are included mainly among the simpler types of the Ranales, Rosales and Malvales. The very great frequency of the palmate leaf, either simple, lobed or compound, among the Ranunculaceae, Saxifragaceae, Hamamelidaceae, Malvaceae and their immediate allies (over half of the palmate lobed leaves in the floras investigated belong here) thus furnishes the most important evidence that modern phylogeny can contribute to a solution of the present problem and confirms the evidence from other sources that the palmate type is indeed the most ancient among Dicotyledons.

As to which of the three palmate forms is the oldest we cannot be quite sure. It is possible that the simple pinnate leaf with closed venation and the veins all converging at the tip of the lamina, a type which is predominant among Monocotyledons and the seed-leaves of Dicotyledons, may be the most ancient condition, from which the lobed form has arisen by a separation and divergence of the veins. The high percentage of palmate lobed leaves in the more ancient fossil floras, however; the primitiveness of the trilacunar node; the numerous cases of reversion of palmate simple to palmate lobed leaves, and the predominance of the palmate lobed form in the more primitive orders whereas the palmate simple and palmate compound types are often characteristic of more highly specialized groups, all point to the conclusion that a three-lobed, palmately three-veined leaf is one of at least very high antiquity. In such a leaf the three independent leaf trace bundles, widely separated at their insertion, probably remained so throughout their course into the lamina. In modern leaves of this type we usually find either three separate bundles in the petiole (fig. 81) or a single three-lobed one (fig. 80). Other leaf types generally possess a much more complicated petiolar system. If the primitive leaf was sessile or nearly so, as most writers agree, it is probable that

the three traces went off pretty directly into the lamina as is shown in our reconstruction (fig. 83).

If the view thus set forth is a sound one we should be able to trace the transitional steps between such a primitive leaf and the various types of foliage which now occur throughout the Angiosperms.

Intermediate conditions between the palmate lobed and the palmate simple are to be found in several genera such as *Acer*, *Rubus*, *Viburnum*, *Sterculia*, *Malus* and others. In fact, the genus *Acer* (figs. 1 to 11) shows in its various species all transitions from simple pinnate to ternately compound. In many such plastic genera and families, of which the *Araliaceae* are another notable example, almost all leaf types may occur in closely related species and it is common to find several of them, with all sorts of intermediate conditions, even on the same plant. In all such cases vigorous growth emphasizes or restores the palmate lobed condition. In such groups as the *Piperaceae*, *Melastomaceae* and others the lobed condition seems to have been entirely lost, although the venation is still palmate. With the loss of the lobes the two lateral veins usually curve inward, sometimes even giving rise to a practically closed venation.

The palmate compound type has evidently arisen from the lobed one simply by an increase in the depth of the sinuses. The various steps may often be traced in the same species or even on one individual as in species of *Acer* (figs. 6 and 7), *Rubus*, the *Araliaceae* and many others. Since most palmately lobed leaves have three main veins, the compound ones derived from them are for the most part trifoliate. In many cases each leaflet of a trifoliate compound leaf becomes compound, in its turn, thus giving rise to the ternately compound type (fig. 11).

The pinnate simple leaf seems to have had its origin from the lobed type through the disappearance of the lobes (palmate simple) and a great reduction or disappearance of the lateral veins. Numberless transitional steps may be found, especially in the more plastic genera (figs. 1, 2 and 3, 12, 13 and 14). Most families which are preponderantly simple pinnate in leaf type have a few species or genera where the two basal veins are especially prominent or in which the leaf is essentially palmate. In certain cases (*Rutaceae* and others) the simple pinnate leaf probably represents the terminal leaflet of a reduced compound leaf.

The pinnate lobed type has apparently been derived from the

pinnate simple by a more or less complete lateral dissection of the lamina, the lobes really representing very large leaf teeth. Transitions may be found in many herbaceous families (figs. 16 and 17).

The pinnate compound leaf evidently originated from the palmate compound, and transitions may frequently be observed in *Acer* (figs. 8 to 11), *Rubus* (figs. 14 and 15) and many other genera. In each case the two lowest leaflets are homologous with the lateral leaflets of the trifoliate type and the terminal leaflet has cut off basally one or more additional pairs. In practically all woody (and therefore more ancient) Dicotyledons the pinnately compound leaf seems to have arisen through this almost meristematic activity of the terminal leaflet. It is essentially a modified palmate leaf rather than a pinnate one, a fact which may explain what we have previously noted, its almost invariable correlation with a multilacunar node. In certain of the *Proteaceae*, however, and a great many herbaceous and semi-herbaceous species leaves which are essentially pinnate compound have had their origin in an actual dissection of the lamina of a simple pinnate leaf.

In the even-pinnate *Leguminosæ* (and possibly in other families as well) the pinnately compound condition seems to have arisen from a palmately two-lobed rather than from a palmately three-lobed type. Transitions may be found from the simple palmate leaf of *Cercis* (fig. 22) through various species of *Bauhinia* (fig. 23) and related genera to forms with two distinct leaflets (fig. 24) which in still others have cut off pairs of leaflets basally to produce the typical even-pinnate type.

FACTORS IN FOLIAR EVOLUTION

The most important factor operative in altering the ancient three-lobed, three-veined palmate leaf seems to have been the origin of the petiole. It is generally agreed that this organ, the last part of the leaf to appear in ontogeny, is also more recent in evolutionary origin than the rest. It may well owe its development to the fact that the early Angiosperm leaf, ever increasing in breadth of lamina, was in need of a greater flexibility than was afforded by a broad sessile base in order to guard against havoc by winds and also, perhaps, to increase transpiration. The primitive leaf with its three traces widely separated in origin passing directly from node to lamina, was thus constricted at its base and its three bundles forced close together in the

petiole. In some cases, as in a few leaves today (fig. 81), they stayed apart, though crowded close together, and diverged again at the base of the lamina (fig. 84). In others they partially fused by their margins (fig. 80). In most instances, however, they became joined together into a continuous cylinder (fig. 82) or were broken up into a ring of numerous strands. This petiolar system sometimes separated into approximately equal portions again at the base of the lamina but seems to have shown an increasing tendency to persist as a single strand, the midrib, sending off numerous branches on both sides. In other words, the midrib is the continuation of the petiole, to which it owes its origin. The approximation of the three traces in the petiole apparently extended down to the node and was responsible for the origin of the unilacunar nodal type which we have seen to be so intimately correlated with the simple pinnate leaf. Among woody plants the unilacunar type is largely confined to the tropics. This seems to be due to the fact that the tropical rain forest leaf is usually large and heavy and provided with a stout petiole, which for mechanical reasons is cylindrical and which thus has a circular leaf scar or point of attachment as opposed to the elongated scar of most temperate woody plants. This narrower point of insertion of course tends to pull the leaf traces more closely together and thus to develop the unilacunar node, which is also produced occasionally by the loss of the two lateral traces.

We are in almost complete ignorance of the other factors operative in the evolution of the leaf. The development of the palmate simple leaf from the palmate lobed one may well have been due, at least in the first instance, to reduction consequent upon loss of vigor or to decrease in size for other reasons. The acquirement of a leathery, xerophytic texture by the leaf is operative in some way to change the lobed leaf into a simple one, as is shown by the almost complete absence of palmate-lobed leaves among woody plants in the tropics (see Table I and tropical species of *Rubus*, figs. 12 and 13). Tropical leaves are often large and are frequently compound but the ultimate foliar unit, whatever it is, is generally narrow in shape and has a stout midrib. The reason for this is not clear, but it may be connected in some way with tropical xerophily.

As to what causes the development of compound leaves we are also uncertain. Such types, however, perhaps from their ability to orient themselves to sunlight, are well represented in warm, dry

regions, as is shown by the abundance in such places of the Leguminosae, Proteaceae and other compound-leaved types. These families may well have acquired their leaf type under a more mesophytic environment (where most of the transitional conditions are found today) and thus have been especially fitted to invade arid regions.

CLIMATIC DISTRIBUTION OF FOLIAR TYPES

The present distribution of leaf types with reference to climate provides us with evidence as to the climatic conditions under which Angiosperms first appeared. A study of Table I shows that the palmate-lobed leaf is conspicuously absent from the woody plants of tropical regions and is developed almost entirely in such forms under a temperate mesophytic environment, a fact of much suggestiveness since we have concluded that this leaf type is the most ancient of all. A number of families, such as the Rosaceae and Saxifragaceae, have numerous palmate species in the temperate zones but are represented in the tropics almost entirely by pinnate forms.

Palmately lobed leaves occur frequently among herbaceous plants in the tropics and, in fact, the distribution of the various leaf types among herbs is much the same under widely different climatic environments. This state of affairs, which we shall see duplicated in the distribution of nodal types in the various regions, is probably due to the fact that herbs, a recent and adaptable form of vegetation, live under very different circumstances from their more primitive woody relatives in that they can pass over adverse conditions underground or as seeds. Woody plants, because of their permanent aerial habit, are much more susceptible to climatic differences and have closer structural correlations with them. It was among such plants that the evolution of the various types of node and leaf undoubtedly took place.

We have brought forward evidence that the multilacunar type of node is primitive and definitely associated with the various forms of palmate leaves; and that the more recent unilacunar type is almost always connected with the simple pinnate leaf. The following table is therefore of interest in showing the distribution, among trees, shrubs and herbs, of the two nodal types in various regions of the globe.

It will be observed that among herbs the proportions of the two nodal types, like those of leaf shape, are not widely different in the

tropics and the temperate regions, although unilacunar species are somewhat more common in the former than in the latter. Among shrubs, however, we may note a much higher percentage of multi-lacunar species in temperate areas than in arid or tropical ones, running

TABLE V

	Species	Trees		Shrubs		Herbs	
		Multi.	Uni.	Multi.	Uni.	Multi.	Uni.
Northern United States	2,811	85	15	69	31	58	42
Rocky Mountains	1,405	90	10	84	16	62	38
Great Britain	1,231	94	6	81	19	56	44
Germany	1,120	97	3	81	19	54	46
Russian Empire	3,676	95	5	70	30	58	42
Alps	1,735	96	4	87	13	57	43
Spain	3,901	91	9	43	57	53	47
Italy	3,069	92	8	67	33	60	40
Flora Orientalis	9,848	71	29	59	41	63	37
Syria	2,570	84	16	54	46	68	32
Egypt	1,138	83	17	53	47	63	37
China	2,075	76	24	67	33		
Japan	542	87	13	63	37		
Patagonia	1,405	84	16	66	34	67	33
Chili	2,160	76	24	67	33	67	33
New Zealand	974	72	28	47	53	61	39
Hongkong	681	69	31	41	59	52	48
Simla	987	76	24	61	39	56	44
Gangetic Plain	996	60	40	60	40	54	46
Florida Keys	466	56	44	50	50	47	53
Australia (extratropical)	5,874	51	49	67	33	63	37
South Africa	7,284	60	40	58	42	45	55
Amazon Valley	2,174	57	43	30	70	38	62
British West Indies	2,191	46	54	46	54	50	50
Nicaragua	1,496	66	34	54	46	58	42
Tropical Africa	10,520	54	46	32	68	39	61
Mauritius	555	45	55	42	58	56	44
Ceylon	1,752	50	50	43	57	36	64
Bombay, Uplands	996	61	39	50	50	50	50
Bombay, Lowlands	1,229	50	50	48	52	46	54
Dutch East Indies	6,246	49	51	40	60	44	56
Malay Peninsula	3,049	49	51	32	68	26	74
Manila	332	66	34	47	53	44	56
Hawaii	508	50	50	41	59	51	49

from 70 per cent or 80 per cent in the former to 30 per cent or 40 per cent in the latter. Trees, however, which are probably the most ancient type of all, show the widest extremes and among them the relative proportion of the two nodal types is very closely correlated with climate. In the great land area of the north temperate zone

from 85 per cent to 95 per cent (averaging 90 per cent or more) of the arborescent species have three or more gaps at the node. This type is also dominant in the temperate non-arid regions of the Southern Hemisphere, such as Chili, Patagonia and New Zealand; and, to a less extent, in upland areas in or near the tropics, as Nicaragua, Simla and the Bombay uplands. In the tropics, however, there is a strong contrast for here 50 per cent or more of the tree species are unilacunar. Almost all the unilacunar arborescent genera are typically tropical in their distribution. Subtropical regions, such as the Florida Keys, the Gangetic Plain and Hongkong, show a percentage intermediate between the two extremes. In South Africa and extra-tropical Australia, the great arid areas of the South Temperate zone, the unilacunar type is only slightly less common than in the tropics. In connection with this concentration of the presumably primitive trilacunar woody type in generally temperate and mesophytic habitats, it should also be borne in mind that most of the genera and families regarded as being particularly ancient are best developed in temperate or warm-temperate regions.

These facts, which are in agreement with a large body of evidence gathered by the writers from other sources, all point strongly to the conclusion that tropical plants are specialized in almost every particular and that the Angiosperms therefore could not have arisen under a tropical environment, as has generally been taken for granted, but must have had their origin in a climate which, though doubtless very equable and devoid of extremes of temperature, was essentially a temperate one. Such a climate, as far as we are able to judge of conditions in the Mesozoic, could only obtain, as a general rule, in upland or mountainous regions. On such a supposition the Mesozoic Angiosperms which we know are to be regarded as plants which had migrated down into the tropical lowlands and swampy areas, where they could readily be preserved as fossils. If the earliest Dicotyledons were indeed largely confined to temperate upland regions (where fossilization could almost never take place), does not this explain why we know of so very few Mesozoic Angiosperms and why these are so diverse and often so highly specialized and far from primitive? And does it not strongly suggest the possibility that on these ancient mountains, about the vegetation of which we know so little, Angiosperms may have been developing in extremely remote times, considerably earlier than the Lower Cretaceous?

PHYLOGENETIC CONCLUSIONS

If the hypothesis which has here been presented is a sound one and the trilacunar palmate leaf type is indeed the most ancient among Angiosperms, the theory which derives these dominant seed plants from Cycad-like Gymnosperms meets with grave difficulty. The Mesozoic Bennettitales, from which many phylogenists believe the Angiosperms to have descended, were unilacunar and possessed, like all Cycads, pinnately compound leaves. The difficulty of deriving from such a leaf the foliar types which prevail among living Angiosperms has been noted by many writers. Wieland¹⁰ suggests that the gap may have been bridged by a fusion of the leaflets of the compound leaf, with the eventual production of a simple pinnate one. But if a palmate leaf was indeed the primitive Angiosperm condition it is difficult to see how it could have arisen from any cycadaceous type. The Conifers, on the other hand, are invariably palmate in their venation. Although the common leaf type is a narrow one with but one or two strands, there are numerous cases in the Araucarineae and Podocarpineae where the leaf becomes broader. In accommodation to this change the vascular tissue increases in amount, but always by a basal multiplication of the strands in palmate fashion rather than by the origin of branches from a midrib (figs. 74 and 75). It is possible to imagine how such a broad-leaved form, developing a trilacunar type of insertion (Agathis is occasionally bilacunar) might easily give rise to the palmate leaf which we have regarded as ancient. Evidence from the leaf certainly favors a coniferous rather than a cycadean stock as ancestral for the Angiosperms.

Information from this source is also important in connection with the ancestry of the Monocotyledons. These plants are almost invariably palmate in their venation, and in many cases are three-veined. In the broad-leaved members of the Potamogetonaceae, Alismaceae, Araceae, Liliaceae, Dioscoreaceae and others we often meet with leaves which are essentially like those of the Piperaceae, Melastomaceae and other palmate Dicotyledons (figs. 76 and 77). The nodal conditions in such forms often suggest the dicotyledonous type, three traces departing to each leaf (fig. 78), and the petiole is

¹⁰ Was the Pterophyllum Foliage Transformed into the Leafy Blades of Dicotyls? Wieland, G. R., *Am. Jour. Science* 38: 451-460. 1914.

also frequently trifasciculate. The cotyledon and early leaves in several families of Monocotyledons have been shown by Chrysler¹¹ and Coulter and Land¹² to have three bundles (fig. 79), apparently a vestige of the more ancient condition. The conspicuous tendency for the cotyledonary veins in the seed-leaves of many Dicotyledons to unite at the tip of the lamina (figs. 21, 27, 28, 38, and 44) producing a closed venation like that of the Monocotyledons, suggests either that the Monocotyledons are the more ancient of the two classes, a conclusion opposed by too much evidence from other sources; or that the leaf in these plants has been developed by a process of reduction much like that gone through by the cotyledons of Dicotyledons and by the mature leaves of certain members of that class. The Monocotyledons apparently had their origin from a palmate dicotyledonous stock, very likely at an early period when the palmate leaf was predominant among all Angiosperms.

SUMMARY

1. The primitive Angiosperm leaf was palmate in type, probably lobed, and was provided with three main bundles which arose separately at the node.

2. This conclusion is based on evidence from palaeobotany, that the palmate leaf was more frequent in the Cretaceous and Tertiary than at present; from morphology, that there is a correlation between the palmate leaf and the multilacunar node and between the pinnate leaf and the unilacunar node and that the former nodal type is the more ancient, that cotyledons and floral leaves are much more frequently palmate than are vegetative ones, and that vigorous growth emphasizes the palmate type; and from phylogeny, that palmate leaves are most frequent in relatively primitive groups and pinnate leaves in more advanced ones.

3. Transitions from the palmate lobed type to all other leaf forms may readily be traced.

4. The chief factor in the evolution of the now dominant pinnate leaf seems to have been the development of the petiole, in which

¹¹ The Development of the Central Cylinder of the Araceae and Liliaceae, Chrysler, M. A., Bot. Gaz. 38: 161-184. 1904.

¹² The Origin of Monocotyledony, Coulter, J. M. and Land, W. J. G., Bot. Gaz. 57: 509-519. 1914.

the three originally distinct leaf bundles were pulled together into a single strand, the midrib.

5. Among woody plants, the multilacunar (more ancient) nodal type predominates in temperate regions and the unilacunar (more recent) in the tropics. The palmate lobed leaf among such plants is also almost entirely confined to temperate regions. These facts, in company with others, indicate that the Angiosperms first appeared under a climate more temperate than tropical, a climate in the Mesozoic probably found only in the uplands. It is suggested that the absence of the earliest Angiosperms as fossils may be due to their confinement to such upland regions, where preservation would be very difficult.

6. Evidence from the leaf strongly favors the view that the Angiosperms sprang from a coniferous (palmate) rather than from a cycadean (pinnate) stock.

7. The Monocotyledons were derived from some ancient palmate group of Dicotyledons.

The writers are much indebted to the authorities of the Gray Herbarium and of the Arnold Arboretum for the use of their libraries and herbaria.

BUSSEY INSTITUTION,
HARVARD UNIVERSITY.

DESCRIPTION OF FIGURES OF PLATES I-IV

FIG. 1. *Acer carpinifolium* Sieb. & Zucc. (pinnate simple).

FIG. 2. *Acer tataricum* L. (palmate simple).

FIG. 3. *Acer ginnale* Maxim., vigorous leaf (palmate lobed).

FIGS. 4 AND 5. *Acer ginnale* Maxim. leaves of less vigorous growth.

FIGS. 6 AND 7. *Acer glabrum* Torr., two leaves from the same twig showing origin of palmately compound type.

FIGS. 8, 9, 10 AND 11. *Acer Negundo* L., series of leaves showing transitions from trifoliate to ternately compound.

FIGS. 12 AND 13. *Rubus negroensis* Elm. and *Rubus benguitensis* Elm., tropical species reduced from primitive type.

FIG. 14. *Rubus odoratus* L., presumably primitive type for the genus.

FIG. 15. *Rubus neglectus* Peck, leaf showing the transition from palmately to pinnately compound.

FIGS. 16 AND 17. *Solanum nigrum* L. and *Solanum carolinense* L. two closely related species showing transition from pinnate simple to pinnate lobed.

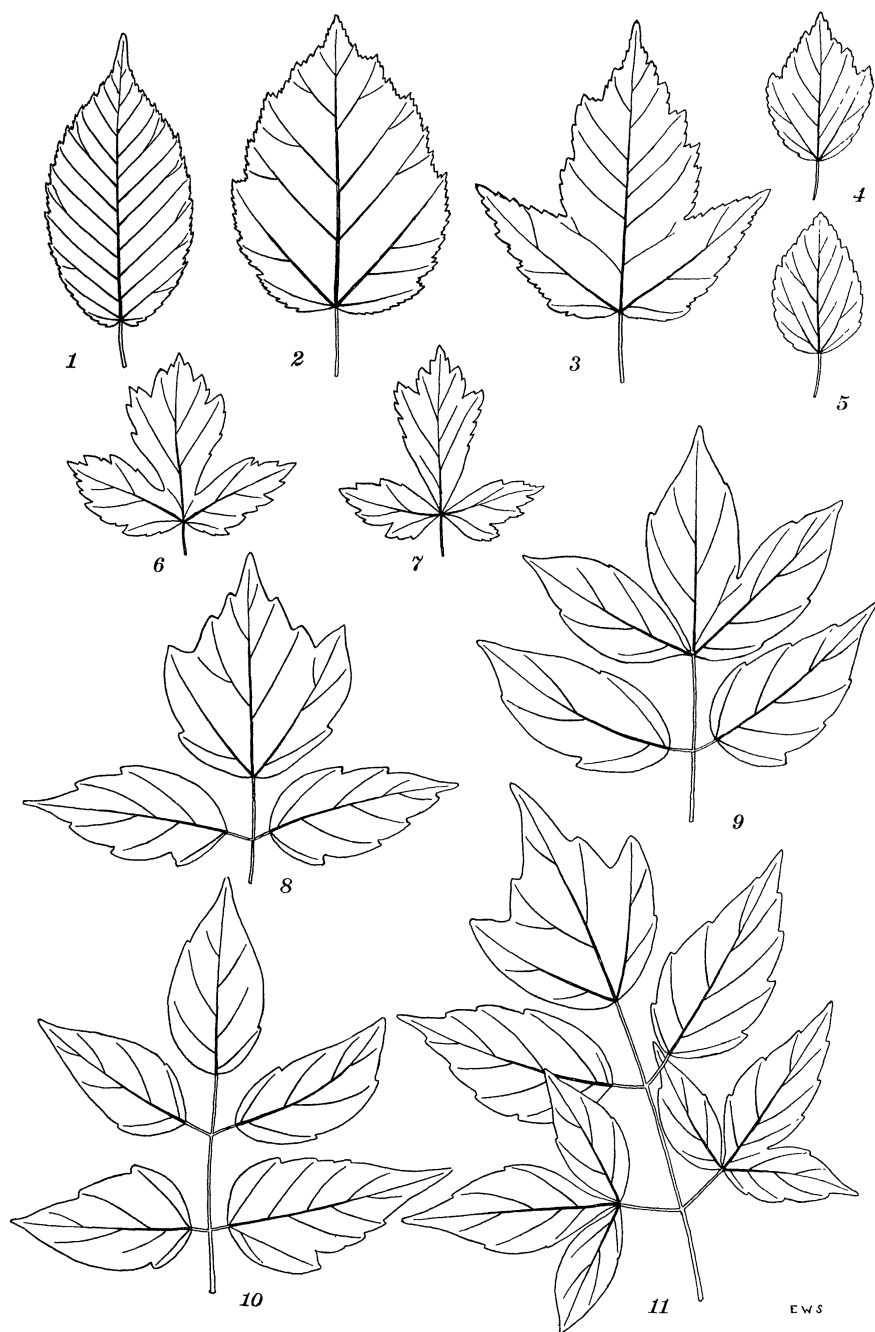
FIGS. 18 AND 19. *Ampelopsis tricuspidata* Sieb. & Zucc., a leaf of vigorous and one of weaker growth.

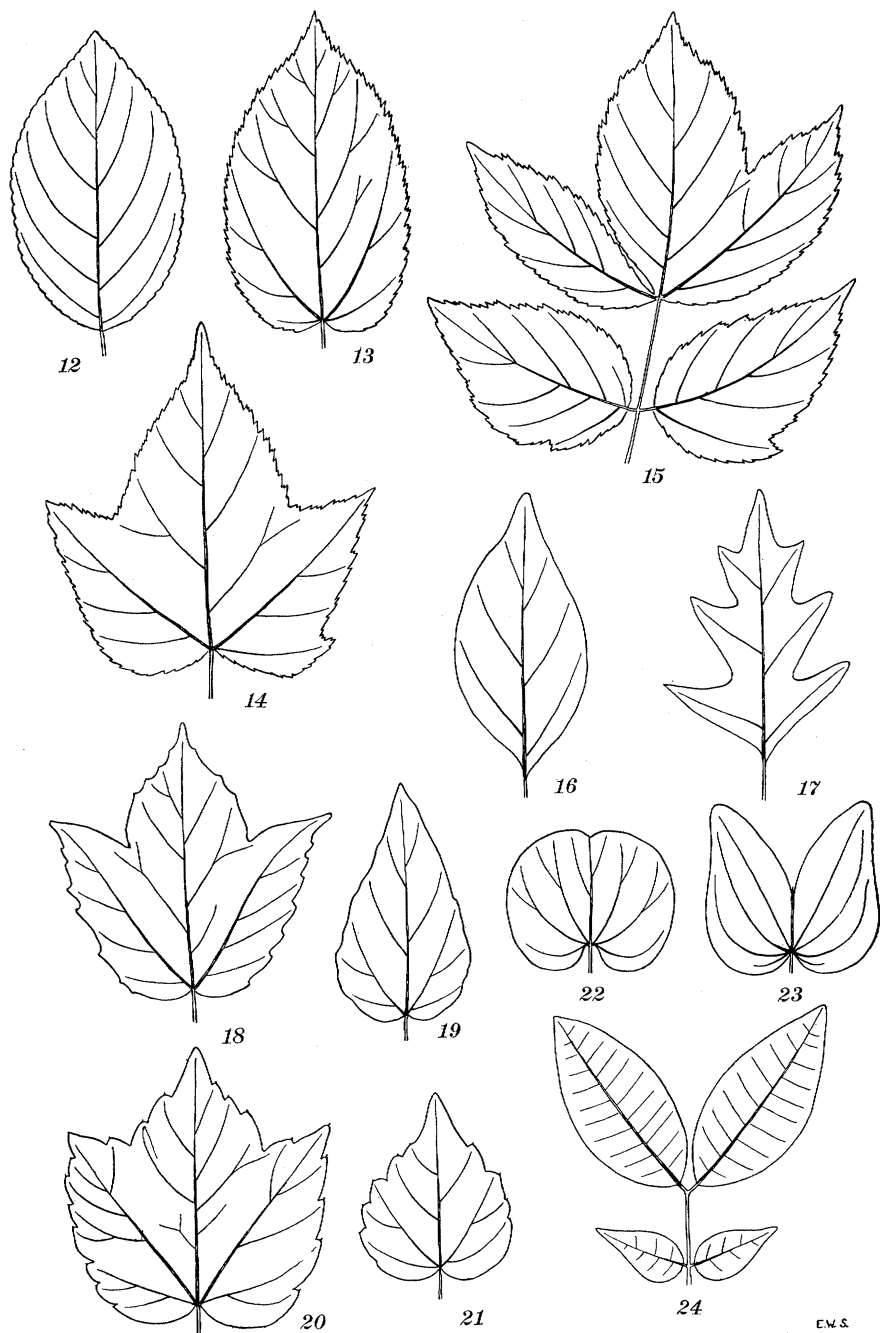
FIGS. 20 AND 21. *Viburnum acerifolium* L., a leaf of vigorous and one of weaker growth.

FIGS. 22, 23 AND 24. *Cercis occidentalis* Torr., *Bauhinia* sp. and *Hymenostegia* sp., series showing origin of the pinnately compound type among certain of the Leguminosae.

- FIG. 25. *Engelhardtia spicata* Blume, floral bract (leaf pinnate compound).
- FIG. 26. *Betula nigra* L., floral bract (leaf pinnate simple).
- FIG. 27. *Carpinus caroliniana* Walt., floral bract (leaf pinnate simple).
- FIG. 28. *Bocconia frutescens* L., floral bract (leaf pinnate lobed).
- FIG. 29. *Dalechampia Passiflora* C. & H., floral bract (leaf palmate simple).
- FIG. 30. *Adhatodia vasica* Nees, floral bract (leaf pinnate simple).
- FIG. 31. *Berberis Bealei* Curt., petal (leaf pinnate simple).
- FIG. 32. *Schizophragma hydrangeoides* Sieb. & Zucc., petal (leaf pinnate simple).
- FIG. 33. *Guichenotia macrantha* Turcz., petal (leaf pinnate simple).
- FIG. 34. *Anisoptera glabra* Kurz, calyx lobe (leaf pinnate simple).
- FIG. 35. *Calycopteris floribunda* L., calyx lobe (leaf pinnate simple).
- FIG. 36. *Mussaenda tenuiflora* Benth., petal (leaf pinnate simple).
- FIG. 37. *Casuarina stricta* Ait., cotyledon (leaf greatly reduced).
- FIG. 38. *Pterocarya fraxinifolia* Spach, cotyledon (leaf pinnate compound)
- FIG. 39. *Betula nigra* L., cotyledon (leaf pinnate simple).
- FIG. 40. *Celtis occidentalis* L., cotyledon (leaf palmate simple).
- FIG. 41. *Grevillea robusta* A. Cunn., cotyledon (leaf pinnate compound).
- FIG. 42. *Antigonon leptopus* Hook., cotyledon (leaf pinnate simple).
- FIG. 43. *Mirabilis jalapa* L., cotyledon (leaf pinnate simple).
- FIG. 44. *Rivinia aurantiaca* Warsz., cotyledon (leaf pinnate simple).
- FIG. 45. *Delphinium formosum* Boiss. & Hook., cotyledon (leaf palmate lobed).
- FIG. 46. *Brassica olearacea* L., cotyledon (leaf pinnate simple).
- FIG. 47. *Crataegus oxyacantha* L., cotyledon, after Lubbock (leaf pinnate simple).
- FIG. 48. *Mimosa pudica* Mill., cotyledon (leaf pinnate compound).
- FIG. 49. *Canarium strictum* Roxb., cotyledon, after Lubbock (leaf pinnate compound).
- FIG. 50. *Euphorbia pulcherrima* Willd., cotyledon (leaf pinnate simple).
- FIG. 51. *Rhus typhina* L., cotyledon (leaf pinnate compound).
- FIG. 52. *Acer saccharum* Marsh, cotyledon (leaf palmate lobed).
- FIG. 53. *Rhamnus cathartica* L., cotyledon (leaf pinnate simple).
- FIG. 54. *Ampelopsis tricuspidata* Sieb. & Zucc., cotyledon (leaf palmate lobed).
- FIG. 55. *Elaeocarpus oblongus* Smith, cotyledon, after Lubbock (leaf pinnate simple).
- FIG. 56. *Tilia americana* L., cotyledon (leaf palmate simple).
- FIG. 57. *Althaea rosea* Cav., cotyledon (leaf palmate lobed).
- FIG. 58. *Passiflora alata* Ait., cotyledon (leaf pinnate simple).
- FIG. 59. *Lecythis Ollaria* L., cotyledon, after Lubbock (leaf pinnate simple).
- FIG. 60. *Aucuba japonica* Thunb., cotyledon, after Lubbock (leaf pinnate simple).
- FIG. 61. *Eucalyptus calophylla* R. Br., cotyledon (leaf pinnate simple).
- FIG. 62. *Argania sideroxylon* Roem. & Schult., cotyledon (leaf pinnate simple).

- FIG. 63. *Diospyros Lotus* L., cotyledon (leaf pinnate simple).
 FIG. 64. *Ipomaea purpurea* Roth, cotyledon (leaf palmate simple).
 FIG. 65. *Eranthemum leuconeurum* Fisch., cotyledon, after Lubbock (leaf pinnate simple).
 FIG. 66. *Coffea arabica* L., cotyledon, after Lubbock (leaf pinnate simple).
 FIG. 67. *Viburnum Opulus* L., cotyledon (leaf palmate-lobed).
 FIG. 68. *Cucumis Melo* L., cotyledon (leaf palmate-lobed).
 FIG. 69. *Senecio multiflorus* DC., cotyledon (leaf pinnate simple).
 FIG. 70. *Tropaeolum majus* L., young leaf, near the growing point.
 FIG. 71. *Tropaeolum majus* L., mature leaf.
 FIG. 72. *Pterospermum Heyneanum* Wall., leaf from coppice shoot.
 FIG. 73. *Pterospermum Heyneanum* Wall., leaf from mature branch (both after Brandis).
 FIG. 74. *Podocarpus Nagi* Pilger, many-veined (palmate) leaf.
 FIG. 75. *Podocarpus Hallii* Kirk, primitive type of leaf, with single bundle.
 FIG. 76. *Sagittaria latifolia* Willd., mature leaf.
 FIG. 77. *Trillium cernuum* L., mature leaf. Both this and the last are essentially like many dicotyledonous leaves in venation.
 FIG. 78. *Trillium cernuum* L., diagrammatic cross section through the node, showing the similarity to the dicotyledonous type.
 FIG. 79. *Agapanthus umbellatus* L'Her., diagrammatic cross section through the seedling, showing the three bundles in the cotyledon and in the first leaf (after Coulter and Land).
 FIG. 80. *Viburnum acerifolium* L., cross section through the petiole.
 FIG. 81. *Ribes rubrum* L., cross section through the petiole.
 FIG. 82. *Ulmus americana* L., cross section through the petiole.
 FIG. 83. Reconstruction of the leaf (with cross section of the node) supposedly primitive for the Angiosperms. The node is trilacunar and the veins depart directly into the lamina without approximation in a petiole.
 FIG. 84. A typical modern palmate lobed leaf. The node is trilacunar but the traces are pulled closely together in a narrow petiole before separating again in the lamina.
 FIG. 85. A pinnate simple leaf. The node has become unilacunar and the single trace continues as a strong midrib.





E.W.S.

